

PAPERS.

7. The Prechordal Portion of the Chondrocranium of *Chimera collicii*. By EDWARD PHELPS ALLIS, JUN., F.Z.S.

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The prechordal portion of the chondrocranium of the adult *Chimera* is directed ventro-anteriorly, and not anteriorly as Hubrecht's (1877) figure of this fish would lead one to suppose. This is unquestionably due to the trabeculae having been first laid down at a marked angle to the parachordals, and to their having retained, to a marked extent, that primitive position, instead of, as in the Selachii, later gradually acquiring a position approximately in the line prolonged of the parachordals. The chondrocranium of *Chimera* at these early stages has unfortunately not been described. It has, however, been described at these stages in certain of the Selachii, and at slightly later stages in *Callorhynchus*, and reference must be made to the conditions in these embryos of these fishes before describing those in the adult *Chimera*.

SELACHII.

In *Acanthias* and *Pristiurus*, and hence probably in all of the Selachii, the cranial flexure is so great when the neurocranium begins to chondrify that, as shown in Sewertzoff's (1899) figures of embryos of these fishes, the parachordals and the enclosed notochord project slightly into the hollow of the mesocephalic flexure (plica encephali ventralis, von Kupffer, 1906). The trabeculae cannot, accordingly, be laid down in the line prolonged of the parachordals, and, preserving their normal relations to the ventral surface of the brain, they at first lie at right angles to the parachordals and slightly posterior to their anterior ends. The marked cranial flexure at this stage also affects the position of all the visceral arches that lie anterior to the hyal arch, and the palatoquadrate and mandibula, which represent either the cartilaginous bar of the mandibular arch alone, or that bar together with parts of the bars of one or more pre-mandibular arches, lie, when first laid down, at right angles to the trabeculae, and hence in a nearly horizontal instead of a

* For explanation of the Plates see p. 143.

vertical position. Because of this, and also because of the relatively much greater development of these bars, they have crowded the bars of the more posterior arches posteriorly to such an extent that their dorsal ends lie in the auditory and spinal regions. The sphenolateral cartilage of either side (alisphenoid, Sewertzoff) lies, at this stage, in the horizontal plane of the parachordals, lateral to the hollow of the plica encephali ventralis. The nervi facialis, trigeminus, and ophthalmicus profundus all run outward postero-dorsal to this cartilage, the oculomotorius and opticus, and apparently also the trochlearis, running outward antero-ventral to it. In slightly older stages an ethmoidal cartilage is developed, which begins at a point ventral to the lateral edge of the trabecula of its side, and ventral to the eyeball, and runs dorso-anteriorly dorsal to the nasal sac.

When the cranial flexure later becomes reduced, there is first formed, in *Pristiurus*, and hence probably in all the Selachii, a pronounced pontial flexure, but this flexure also becomes later reduced, and almost entirely disappears in the adult. During these changes the trabeculae curve forward, or forward and upward, following the curved ventral surface of the brain, and this change in their direction and position affects the mandibular branchial bars, which, retaining their perpendicular relations to the trabeculae, swing downward and forward, and so acquire a position vertically beneath the latter cartilages. These mandibular bars had apparently already become attached to the hyal bars by connective or ligamentous tissues, and the latter bars and the bars of the branchial arches had become similarly attached to each other both dorsal and ventral to the branchial clefts. When the mandibular bars swung downward and forward they accordingly pulled on the more posterior bars, but as the dorsal ends of the hyal and branchial bars, and the ventral ends of the latter bars, had become attached to tissues in the region where they lay, they were relatively fixed in position, and the middle elements, alone, of each bar could be moved forward, the branchial clefts of course shifting forward with them. This gave rise to the sigma form of branchial bar actually found in the adults of these fishes. In the Teleostomi, where there is but little cranial flexure when the neurocranium begins to chondrify, the trabeculae are laid down in the line prolonged of the parachordals. The mandibular branchial bars were accordingly there laid down approximately in a vertical position, and the bars of the more posterior arches, not being pushed posteriorly by them, retained their primitive attachment in the cranial region. The sigma form of arch was accordingly not impressed upon the bars of the branchial arches of these fishes.

The trabeculae, in the older embryos described by Sewertzoff, have fused with each other in the median line anterior to the pituitary body, and been prolonged, as a wide median plate, to the nasal region. There the plate contracts abruptly and is

prolonged between the nasal sacs as a narrow rostral stalk in *Acanthias*, but as a wide internasal plate in *Pristiurus*, the two structures evidently being, as they are said by Sewertzoff to be, strictly homologous. Anterior to the nasal sacs this stalk or plate expands laterally, on either side, and in *Acanthias* forms the rostral plate of Sewertzoff's descriptions, a median keel-shaped ridge projecting ventrally from its ventral surface and being continuous with a similar ridge on the ventral surface of the rostral stalk. In *Pristiurus* the rostral plate is said by Sewertzoff to be represented in the three bars of the rostral basket, the keel of the plate of *Acanthias* representing the middle bar of the basket of *Pristiurus*, and the lateral portions of the plate representing the lateral bars. This I consider to be an erroneous interpretation of the conditions, the rostral plate of *Acanthias* certainly including, with the three bars of the rostral basket of *Pristiurus*, the narrow strip of cartilage that, in the latter fish, runs laterally immediately anterior to the nasal sac and is called by Sewertzoff the cartilage *c*. This cartilage *c* is said by Sewertzoff to not yet be developed in the oldest embryos of *Acanthias* examined by him, but to be found in the adult as a bar of cartilage that cuts the fenestra olfactoria of embryos into two parts, the lateral one being the definitive foramen olfactorium, and the mesial one the basal communication canal of Gegenbaur's (1872) descriptions of the adults of certain of the Selachii. The large perforation of either side of the floor of the rostral basket of *Pristiurus* is accordingly said, in accord with Gegenbaur's earlier conclusion, to be a basal communicating canal strictly similar to the one found in the adult *Acanthias*, but greatly enlarged and shifted forward; this large perforation of the rostral basket of this fish, and the large opening that actually transmits the nervus olfactorius, thus together representing the fenestra olfactoria of embryos of *Acanthias*. In an earlier work (Allis, 1913), I came to the conclusion that these perforations of the rostral basket of the Carchariidæ and Scylliidæ were not basal communicating canals, and that they were "probably . . . simply defects in the cartilage (of the rostrum) due to the presence of the large number of ampullæ found in this region in these fishes," and this conclusion I consider to be confirmed by conditions that I have since found in one specimen of *Acanthias blainvillii*. In this specimen there is a basal communicating canal in normal position on each side of the head, and on one side of the head the rostral process is perforated by an irregular opening certainly strictly homologous to the perforations found in the Carchariidæ and Scylliidæ; and there are numerous ampullæ lying opposite the perforation.

The cartilage *c* of *Pristiurus* thus certainly corresponds to a part of the rostral plate of *Acanthias*, and the two cartilages of *Pristiurus*, one on either side of the head, can, for convenience, be together called the rostral plate, although they represent only a part of that plate as found in *Acanthias*. This plate and its stalk,

in both these fishes, lie, at this age, in the line prolonged of the trabecular plate, and each lateral end of the narrow plate of the one (*Pristiurus*), and each postero-lateral corner of the broad plate of the other (*Acanthias*), turns dorso-posteriorly as a band-like process which passes dorsal to the nervus olfactorius and dorsal to the nasal sac, and, fusing posteriorly with the anterior ends of both the ethmoidal and sphenolateral cartilages, forms the dorsal boundary of the opening that transmits the nervus olfactorius; the sphenolateral cartilage quite certainly not taking any part in the formation of the actual boundary of the opening. This opening will be hereafter called the fenestra olfactoria in both these fishes, notwithstanding that it is said by Sewertzoff to be later subdivided into a foramen olfactorium and a basal communicating canal in *Acanthias*, and to represent the definitive foramen olfactorium in *Pristiurus*.

The nasal capsule of either side, as shown in Sewertzoff's figures, is represented by a curved plate of cartilage which encircles the basal portion of the anterior and lateral surfaces of the nasal sac and projects ventrally from the ventro-lateral surface of the rostral plate. It is completely fused, by its dorsal edge, with the rostral plate, but its position suggests that it is primarily an independent cartilage secondarily fused with that plate. Parker (1876) shows the nasal capsule in a somewhat different condition in *Scyllium*, but the figures given by him are difficult to comprehend and not readily compared with those given by Sewertzoff. The capsule, however, as shown by both these authors in these several fishes, lies ventro-lateral to the trabecular and rostral cartilages, and where, in these or others of the Selachii, the capsules of opposite sides have been pressed together so as to meet in the median line and there be separated only by a septum nasi, that septum lies ventral to the trabeculae, as shown in Parker's sectional views of *Scyllium* and in Gegenbaur's sectional view of *Mustelus*. The trabeculae, in each of these latter fishes, curve dorsally above the nasal sacs and are furnished with a deep median subethmoidal keel which extends ventrally between the sacs and is shown, in each case, as largely fenestrated in its middle portion. Parker (1876, p. 207) apparently considered this internasal septum to be an upgrowth of the trabecular cartilage, but Parker and Bettany (1877) say that the trabecular plate gradually rises to the level of the nasal roof and there suddenly narrows and is confluent with the internasal septum, this seeming to mean that the septum lies ventral to the trabeculae, as I consider it to do. This difference in interpretation, by these two authors, of identical conditions is apparently due to Parker having considered the trabeculae to be continued forward in the ventral edge of the subethmoidal keel, while Parker and Bettany consider them to be represented in the plate from which that keel descends, that is in the trabecular crest of Parker's descriptions.

A ventro-lateral trabecular process, lying antero-ventral to

the nasal sac, is shown, slightly developed, in Parker's (1876) figures of embryos of *Scyllium*, the process there projecting laterally from the ventral edge of the subethmoidal keel. This process is called by Parker the cornu trabeculae; but two other cartilages on each side of the head are also so designated by him, one being the cartilage *c* of Sewertzoff's descriptions, and the other the lateral bar of the rostral basket. This ventro-lateral trabecular process is not shown or described by Sewertzoff even in the oldest of his embryos, but that it is not peculiar to fishes in which there is a subethmoidal keel is shown by the conditions in the adult *Chlamydoselachus*, where the process is found well developed and there forming the anterior portion of the solum nasi of my descriptions of that fish (Allis, 1913).

The beginnings of a process that lies postero-ventral to the nasal sac is shown, in Sewertzoff's figures, at the ventro-lateral corner of the ethmoidal cartilage, and it is apparently it alone that is later prolonged into the important ventro-latero-posteriorly directed process that is currently called the antorbital or ethmo-palatine process. This antorbital process is, however, said to be formed, in certain other fishes and in higher vertebrates, by an outgrowth of the trabecular cartilage. It is therefore possible that there are two processes here, one of ethmoidal and the other of trabecular origin. If so, they are indistinguishably fused with each other in the Selachii, and to avoid confusion I shall call the process, whatever its origin, the ventro-lateral antorbital process, the entire antorbital process being considered to form the anterior wall of the orbit and to include both this ventro-lateral process and a more or less developed dorso-lateral process found in the adults of most fishes and frequently called the antorbital or preorbital process.

The sphenolateral cartilage has, in the oldest embryos of *Acanthias* described by Sewertzoff, grown forward and fused with the ethmoidal cartilage, and its supraorbital ridge, turning downward at its anterior end, forms the dorsal portion of the lateral edge of the antorbital process, that portion of that edge corresponding to the well-developed dorso-lateral antorbital process found in certain other fishes. The ramus ophthalmicus superficialis trigemini and the nervus ophthalmicus profundus both, in younger embryos, run forward through the orbit and then dorsal to the nasal sac, passing external to the ethmoidal cartilage, between the dorso-lateral and ventro-lateral antorbital processes. But when the sphenolateral and ethmoidal cartilages fuse, the two nerves and an accompanying vein and artery become more or less enclosed between them, either separately or together. The nasal vein, which comes from the nasal pit to fall into the orbital venous sinus, also either becomes enclosed between these two cartilages or is enveloped in the lateral edge of the ethmoidal cartilage alone.

The nasal sac of embryos of the Selachii thus lies between four processes, more or less developed, two being derived from the

trabeculae and lying anterior to the sac, and two derived either from the trabecular, ethmoidal, or sphenolateral cartilages and lying posterior to the sac; and the nasal capsule, when it develops, also lies between and is more or less fused with these processes. The dorsal trabecular process and the ethmoidal constituent of the dorso-lateral antorbital process always fuse with each other above the nervus olfactorius, so forming the dorsal boundary of the fenestra olfactoria, and they also form, together with the sphenolateral cartilage, the lateral wall of the cavum praecerebrale of my descriptions (Allis, 1913). The two ventral processes may also fuse with each other at their outer ends, so forming a perforated plate which lies beneath the nasal sac, the perforation of this solum nasi being closed by membrane and representing an unchondrified portion of the nasal capsule.

The ventro-lateral antorbital process and the two prenasal processes of the Selachii are found in embryos of *Ceratodus*, the former being called by Greil (1913) the processus antorbitalis and the two latter the dorso-lateral and the anterior or lateral trabecular cornua. No dorso-lateral antorbital process is shown in Greil's figures of embryos of this fish, but it is shown by Fürbringer (1904) in a figure of the adult *Ceratodus*, the process there apparently arising as a lateral process from the dorsal end of the posterior wall of the nasal capsule, and being called by Fürbringer the preorbital process. The septum nasi of *Ceratodus* apparently lies dorsal to the trabeculae, as it does in the Teleostei, Holostei, and Crossopterygii, the septum in these several orders of fishes accordingly not being the homologue of the septum in the Plagiostomi, unless it be that the internasal prolongation of the trabeculae of embryos of the former fishes corresponds to the ventral edge of the subethmoidal keel of embryos of the Plagiostomi and not to the rostral stalk and rostral plate, which seems quite probable.

CALLORHYNCHUS.

In *Callorhynchus*, as in *Acanthias* and *Pristiurus*, the trabeculae are first laid down practically at right angles to the parachordals, as consideration of Schauinsland's (1903) figures of a 60 mm. embryo of this fish makes plainly evident. This is due, as in the Selachii, to the marked cranial flexure at this period; but in *Callorhynchus* the anterior portion of the brain, instead of recurving upward and forward as if seeking to reacquire a position in the line of the axis of the body, projects ventro-anteriorly in a straight line. Related to this retention, in this position, of this anterior portion of the brain, the eyeballs of the adult fish lie dorso-anterior to it; but whether it is this position of the brain that has forced the eyeballs to pass antero-dorsal to it, or the precocious development of the eyeballs that has prevented the brain from recurving upward, is not apparent.

The trabeculae fuse to form a wide trabecular plate which,

instead of curving gradually upward and forward, as in the *Selachii*, follows the straight line of the ventral surface of the brain until it reaches what Schauinsland considers to be the anterior end of the cranial cavity. There the trabecular plate, which at this age is still procartilaginous in its anterior portion, contracts abruptly to a narrow procartilaginous bar which lies at a marked angle to the trabecular plate, being directed dorso-anteriorly instead of ventro-anteriorly. This narrow procartilaginous bar is called by Schauinsland the "Septum im vorderen Schädelabschnitt," but it is evident that it is the strict homologue of the rostral stalk of the *Selachii*. The three rostral processes of Schauinsland's descriptions are all shown arising from this stalk, the median process from its dorsal end and the two lateral processes from its lateral edges at about the middle or dorsal third of its length. A short, plate-like subethmoidal keel has begun to develop on the external and hence morphologically ventral surface of the stalk.

From either side of the dorsal end of this rostral stalk, a band-like process runs laterally and then posteriorly, and, spreading dorsally and ventrally, fuses with the procartilaginous anterior portion of the ethmoidal cartilage, which cartilage forms the antorbital process and the anterior wall of the orbit. This band-like process is accordingly a dorso-lateral trabecular process, similar to that in the *Selachii*, and the large opening enclosed between it, the rostral stalk, and the ethmoidal and trabecular procartilages should be primarily a simple fenestra olfactoria similar to that in the *Selachii*, but, even in the youngest embryos described by Schauinsland, the dorsal portion of the fenestra has apparently been already converted into a fenestra nasalis by the beginning of the development of the nasal capsule.

The development of the nasal capsule is not readily comprehended from the several figures given by Schauinsland. In the figures of the 60 mm. embryo (figs. 130-131) the capsule is not indicated by index-letters, but the lateral edge of the anterior opening of the cranial cavity is irregular, the dorsal portion projecting anteriorly beyond the ventral portion and occupying the place in which, in the 85 mm. embryo (figs. 124-126), the nasal capsule is shown. In an embryo said to be older than the 85 mm. one, but of which the length is not given, the nasal capsule is a dome-shaped protuberance of the dorso-lateral portion of the cranial wall immediately posterior to the actual anterior opening of the cranial cavity. Ventral to this so-called capsule the lateral wall of the cranial cavity runs evenly onward to the edge of the anterior opening of the cranial cavity, the capsule apparently not extending into this part of the cranial wall notwithstanding that the ventral portion of the nasal sac must certainly lie internal to it. The nasal sac also quite certainly does not project upward into the dome-shaped protuberance, that protuberance apparently lying above the nasal sac and resembling a dome-shaped swelling that I find, in the

adult *Mustelus*, lying posterior to the foramen olfactorium and directly above the lobus olfactorius.

The dome-shaped protuberance of *Callorhynchus*, the so-called nasal capsule, always lies, at all stages of its development, in the region between the bases of the median and lateral rostral processes, and as the capsule increases in size the bases of the rostral processes are correspondingly separated from each other, and the anterior opening of the cranial cavity carried correspondingly forward; but whether this growth of the cranial wall takes place posterior to the fenestra olfactoria of the 60 mm. embryo, or is due to growth anterior to that fenestra, cannot be told from the figures. In the one case the nasal sac, which certainly lay primarily anterior and external to the cranial cavity, would have been pulled relatively backward into the anterior end of that cavity; the fenestra olfactoria of the 60 mm. embryo would remain morphologically unchanged, but would change in function from a fenestra olfactoria to a fenestra nasalis; and the so-called nasal cartilages of Schauinsland's figures would represent detached pieces of an undeveloped nasal capsule. In the other case, the nasal capsule would be developed as a direct anterior, but morphologically ventral, prolongation of the cranial walls, a fenestra nasalis gradually developing external to the fenestra olfactoria of the 60 mm. embryo. The conditions in the adult *Chimera* decidedly favour this latter view, but one of Schauinsland's figures of *Callorhynchus* equally decidedly favours the former view. The figure in question (fig. 165) gives a median vertical sectional view of an embryo older than the 85 mm. one, and shows the brain in place in the cranial cavity. The trabeculæ are shown lying in the line prolonged of the parachordals, which is not in accord with the figures of other embryos both older and younger than this one. The septal cartilage is shown as a simple rostral stalk, while in the younger, 85 mm. embryo, it is already an important plate-like structure the posterior portion of which corresponds to the rostral stalk of the 60 mm. embryo, and the anterior portion to the subethmoidal keel of that stalk. The rostral stalk of the embryo shown in figure 165 projects dorso-posteriorly, instead of, as in the other embryos, dorso-anteriorly, and the ventral portion of the nasal sac is shown extending forward anterior to the level of the base of the median rostral process and close to the ventro-anterior corner of the chondrocranium. The nasal sacs, as here shown, must accordingly project beyond the anterior openings of the cranial cavity, if those openings are found in this embryo at all in the positions that they have in the other embryos, both older and younger, and furthermore, they must lie dorsal to the trabeculæ, as they do in *Ceratodus* and the Teleostei, instead of ventral to the trabeculæ, as they do in the Selachii and as they must also in *Callorhynchus* if the septum nasi of this fish lies ventral to the rostral stalk, as shown in Schauinsland's other

figures. There would accordingly seem to be some error in this figure 165.

The ethmoidal cartilage, as shown in these embryos of *Callorhynchus*, arises from the trabecular plate posterior to the fenestra olfactoria of its side, and runs dorsally and then anteriorly to meet and fuse with the band-like dorso-lateral trabecular process. At its ventral end the ethmoidal cartilage gives off a lateral process which, even in the earliest stages shown by Schauinsland, has already fused completely with the palato-quadrata. The sphenolateral cartilage grows forward dorsal to the orbit, and in the 60 mm. embryo, where it is still pro-cartilaginous, bifurcates anteriorly, one end passing dorsal and the other ventral to the ramus ophthalmicus superficialis trigemini, which nerve includes the lateralis fibres destined to supply the latero-sensory and ampullary organs of the region. The ventral one of these two ends of the sphenolateral cartilage has already fused, in this embryo, with the ethmoidal cartilage internal to the ramus ophthalmicus superficialis, and the dorsal end also later fuses with that cartilage but external to the ophthalmicus superficialis, this nerve thus being enclosed in a foramen and a dorso-lateral antorbital process being formed. This process is called by Schauinsland the preorbital process, and both it and the postorbital process are said by him to be primarily independent pieces of cartilage. Concomitantly with the formation of this process and the related foramen, a roof of cartilage has been formed over the nervi ophthalmicus superficialis trigemini and ophthalmicus profundus, enclosing them in a median canal called by Schauinsland the ethmoidal canal. This canal is evidently formed by the coalescence, in the median line, of two canals, one on either side of the head, each of these canals being formed by the roofing over of the groove that, in the Selachii, lodges the corresponding portion of the ramus ophthalmicus superficialis trigemini. In certain specimens of *Chlamydoselachus* I find these grooves partially roofed, either by lips of cartilage that project toward each other from the edges of the grooves, or by nodules of cartilage suspended in membranous strands that stretch across the grooves; and if this roofing process were to be completed and the grooves so formed pressed together in the median line, a median canal would be formed the roof of which would form the actual roof of the cranium and its floor the roof of the cranial cavity.

A remnant of the fenestra præcerebralis of my descriptions of the Selachii (Allis, 1913) is found, as will be later fully explained, in the small median opening marked *t* in Schauinsland's figures 124 and 125, and said by him to be a "Spalte, welche das Schädeldach von dem vorderen ethmoidalen Teil des Schädels trennt." The two large openings in the cranial roof that are called by Schauinsland the anterior and posterior divisions of the primarily single "Præfrontallücke," are not parts of the fenestra

præcerebralis, and hence not parts of the Præfrontallücke of Gegenbaur's (1872) descriptions of the Selachii. The cavum præcerebrale, which in the Selachii lies directly anterior to the fenestra præcerebralis, cannot be represented in any part of the ethmoidal canal, for, aside from the origin of that canal as above explained, the floor of the canal is not formed by the trabeculæ, while the floor of the cavum præcerebrale is. The hind end of the ethmoidal canal is shown, in Schauinsland's figure 165, lying but slightly anterior to the anterior surface of the mid-brain. If this figure is correct, the membranous mesial walls of the orbits must accordingly, even in the oldest embryos considered by Schauinsland, be separated from each other by a considerable interval.

The chondrocranium of embryos of *Callorhynchus* thus apparently owes the several points in which it differs from that of the Selachii mainly, if not wholly, to the fact that that portion of the central nervous system that lies anterior to the plica encephali ventralis not only projects ventrally or antero-ventrally at the time when the trabeculæ are laid down, but that, for some reason, it has continued to lie in that position instead of later gradually curving forward or forward and upward. The trabeculæ still apparently seek to curve upward into the line prolonged of the parachordals, but, because of the interference of the overlying brain, this upward curve is found immediately anterior to the lobi olfactorii instead of, as in the Selachii, in the pituitary region.

The mandibular branchial bars were, doubtless laid down primarily at right angles to the trabeculæ, and hence, as in the Selachii, in a nearly horizontal position, but as the trabeculæ later grow downward and forward instead of, as in the Selachii, curving gradually forward or forward and upward, the mandibular bars have been distorted. The dorsal ends of the processus oticus and basilaris, the latter representing the primitive dorsal end of the arch, apparently remain approximately in their primitive positions in relation, respectively, to the lateral wall of the otic capsule and the trabeculæ, but they have been stretched out into long cartilages by the marked ventro-anterior growth of the trabeculæ, and the epal (quadrate) and ceratal (mandibula) elements of the arch lie in the region of the antorbital process. This will be again referred to when describing the conditions in *Chimaera*. Because of this distortion and change in position of the mandibular branchial bars, the branchial bars of the more posterior arches have also been carried forward and somewhat downward without having been previously pushed backward to the extent that they were in the Selachii, and the dorsal ends of the anterior branchial bars are shown lying in the cranial region in Schauinsland's oldest embryos. The sigma form of arch has, however, been impressed upon their dorsal ends, but not upon their ventral ends.

CHIMÆRA.

1. *Neurocranium.*

In a six-month embryo of *Chimæra collicii*, Dean (1906, p. 108) shows the trabeculæ projecting ventro-anteriorly at a marked angle to the parachordals, which would seem to establish that when first chondrified they lay, as they do in *Callorhynchus*, approximately at right angles to the parachordals. In the adult, the conditions shown by Dean in this embryo still persist to a marked extent, for, as shown in the accompanying figure (Pl. I. fig. 2), the line of the vertebral column, if prolonged, would pass approximately across the dorsal edge of the postelinoid wall and issue from the cranium somewhat dorsal to the base of the median rostral process, the larger part of the prechordal portion of the cranium projecting ventro-anteriorly below this line at an angle of about 30°.

Because of this position of the trabeculæ, the mid-ventral line of the chondrocranium of the adult *Chimæra* projects ventro-anteriorly, and from the level of the foramen magnum to the level of the fenestræ nasales it is slightly curved, the hollow of the curve presented ventro-posteriorly. Anterior to the level of the fenestræ nasales, the mid-ventral line changes abruptly in direction, running at first dorso-anteriorly and then ventro-anteriorly and ending at the anterior end of the short beak-like process of the chondrocranium. This latter process is morphologically subnasal in position, as will be later explained, but as it has the appearance, in lateral view, of being prenasal, it may be called the prenasal process.

Beginning at about the level of the middle of the orbit and extending forward to its anterior edge, there is a median, longitudinal, gash-like groove which lodges the degenerated tissues of the extracranial portion of the hypophysis, the groove being deepest at its posterior end and gradually vanishing anteriorly. This groove represents a persisting remnant of the hypophysial fenestra, that fenestra being, in the adult, completely closed toward the cranial cavity, as it apparently was even in the chondrocranium of the sixth-month embryo shown by Dean. Starting lateral to this groove, on either side, a pronounced but low and rounded ridge runs antero-laterally to the level of the ventral end of the antorbital wall, where it turns somewhat abruptly antero-ventrally and but slightly laterally and bears on its end an articular facet and an articular head, the former lying directly mesial to the latter and both surfaces giving articulation to the mandibula. From the anterior edge of the articular facet the narrow ventro-lateral edge of the chondrocranium runs antero-mesially in a curved line, concave ventrally, till it reaches a point slightly anterior to the ventral edge of the fenestra nasalis, where it turns anteriorly and becomes the ventral edge of the beak-like prenasal process.

Between the mandibular articular facets of opposite sides, the ventral surface of the chondrocranium is deeply concave, this concavity lying in the ethmoidal region and being traversed by the raised median longitudinal ridge of the fused trabeculae. Anterior to this large subethmoidal depression there is a smaller, subnasal one which lies in the hollow of the beak-like prenasal process, the two depressions being separated by a V-shaped ridge, each arm of the V running antero-laterally from the projecting ventro-posterior corner of the subethmoidal keel. The anterior dental plates lie against the dorsal wall of the anterior half of the subnasal depression, the posterior dental plates lying against the anterior border of the subethmoidal depression. From the bottom of the posterior half of the subnasal depression a tough pad of tissue arises and projecting ventrally fills the space between the dental plates.

The bottom of the large subethmoidal depression is separated by the raised ridge of the fused trabeculae into two parts, each triangular in shape, and as each depression lies beneath the lateral portion of the ethmoidal cartilage it may be called the ectethmoidal depression, the two ectethmoidal depressions forming the large subethmoidal one. Each ectethmoidal depression is traversed by the nasal vein of its side, this vein, in some specimens, lying in a pronounced groove at the bottom of the depression. This vein comes from the nasal capsule and the regions anterior to it, and is directly continuous, in the nasal capsule, with a vein that enters the *cavum cranii*, accompanying the *nervus olfactorius*, and joins a vein that issues from the cranial cavity through the foramen for the *nervus vagus*. The nasal vein, running posteriorly from the nasal capsule, first traverses a canal that leads from that capsule through the anterior wall of the ectethmoidal depression, then receives a branch that has traversed the overlying cartilage through a small foramen, and then itself traverses a foramen in the posterior wall of the ectethmoidal depression to enter the orbit and fall into the orbital venous sinus. The ectethmoidal depression of this fish thus corresponds, in general position and in its relations to the nasal vein, to the ectethmoidal chamber of my descriptions of *Chlamydoselachus* (Allis, 1913), that chamber being, in certain of the *Selachii*, an open fossa which may, as in *Heptanchus*, be in direct communication with the cranial cavity through the basal communicating canal of Gegenbauer's descriptions. There is, in *Chimera*, no indication of this latter canal, but it is perhaps worthy of note that in *Lepidosiren* there is, in just this region, a median perforation of the *basis cranii* (Bridge, 1898).

At the postero-mesial corner of the ectethmoidal depression of *Chimera*, near the summit of the ridge that there bounds the depression, there is a groove which leads postero-mesially to a canal which traverses the cartilage of the *basis cranii* and transmits the efferent pseudobranchial, or so-called anterior carotid artery, this canal opening on the dorsal surface of the cartilage

in the region of the line of attachment of the membranous inter-orbital wall, and directly ventro-lateral to the foramen by which the nervus opticus traverses that membranous wall.

The foramen opticum lies directly dorsal to a well-marked and rounded transverse ridge on the floor of the cranial cavity, this ridge marking the anterior end of the pituitary fossa and hence being the presphenoid bolster of my descriptions of the Selachii. The cranial cavity is here abruptly constricted, latero-mesially, and this constriction, in its ventral portion, is produced by the pinching in of the mesial membranous walls of the orbits, the membrane of either orbit being pinched inward and downward so that the internal surface of its ventral portion lies closely upon the cartilage of the basis cranii. The membrane there usually, but not always, becomes adherent to the cartilage, and a second line of attachment of the membranous cranial wall, lying mesial to the primitive line, is acquired. A depression is thus formed in the ventral portion of the outer surface of the membranous wall of each orbit, and it is filled with tough fatty connective tissue. The original line of attachment of the membranous wall forms the ventro-lateral edge of this depression, and lies lateral to the foramen for the efferent pseudobranchial artery, while the secondary line of attachment lies mesial to that foramen, the membrane covering the foramen. Having issued from its foramen, the efferent pseudobranchial artery runs posteriorly beneath the covering membrane and issues in the cranial cavity at the base of the posterior wall of the depression, there lying posterior to the nervus opticus. It then immediately gives off a recurrent branch which perforates the posterior wall of the depression, traverses the tough fatty tissue that fills the depression, and, joining the nervus opticus, accompanies that nerve to the eyeball. After giving off this branch, the pseudobranchial artery turns mesially and immediately separates into anterior and posterior cerebral arteries.

When the secondary attachment of the membranous orbital wall to the dorsal surface of the basis cranii is not strong, the pseudobranchial foramen opens directly into the cranial cavity, but when the attachment is strong it opens external to that cavity but beneath the covering membrane. The nervus opticus, after issuing from its foramen, lies directly upon this adherent membrane, and the membrane may there become thinned to such an extent that, in dissections not carefully made, the pseudobranchial foramen appears as a perforation of the sub-orbital shelf lying wholly external to the interorbital wall; this apparently having been the condition in the specimen examined in connection with my earlier work on the arteries of this fish (Allis, 1912), where the foramen is said to open external to the cranial wall. The foramen however lies, morphologically, in the actual floor of the cranial cavity, as it is shown in Schauinsland's figure of an embryo of *Callorhynchus*. In the Selachii this foramen always lies, in all the specimens that I have

examined, dorsal to the trabecule, and where there is a sub-orbital shelf it lies dorsal to that shelf. This foramen of *Chimæra*, which is quite unquestionably the homologue of the foramen in the *Selachii*, must then have become surrounded by and quite deeply enclosed in the dorso-lateral edge of the trabecula, the membranous lateral wall of this part of the neurocranium thus lying lateral to it and the foramen appearing to lie in the floor of the cranial cavity. The foramen is not shown in Dean's figure of an embryo of *Chimæra*, doubtless because it is hidden, in dorsal view, by the supraorbital portion of the cranial wall.

The branch of the pseudobranchial artery that accompanies the nervus opticus to the eyeball was called by me, in the earlier work just above referred to, the arteria ophthalmica magna, this identification of the artery being based on its apparent origin, in a dissection in which the tissues had evidently been torn, from the pseudobranchial artery before that artery enters the cranial cavity. This is, however, an error, the artery quite certainly being the arteria centralis retinæ, or optic artery, of my descriptions of the *Selachii*, and no arteria ophthalmica magna being found in this fish.

At the hind end of the orbit five foramina, lying close together, perforate the cranial wall and transmit the nervi profundus, trigeminus, buccalis lateralis, facialis, and abducens. The foramen for the facialis is always separated from the other foramina by cartilage, and the foramen for the abducens usually so separated, the other three nerves usually issuing through a single foramen but being separated from each other by membrane. Dorsal to these foramina there is a large foramen for the ramus ophthalmicus superficialis*, and two foramina that lie near the edge of the membranous mesial wall of the orbit, one of them transmitting the nervus trochlearis and the other a venous vessel which is doubtless the anterior cerebral vein of my descriptions of *Amia* and the *Teleostei*. Slightly anterior to the five foramina that transmit the trigeminus, facialis, and abducens nerves there is the foramen for the nervus oculomotorius, which lies at the edge of the membranous mesial wall of the orbit, and ventro-lateral to that foramen there is a small foramen for the pituitary vein, this latter foramen opening into the pituitary fossa. The vein that traverses this latter foramen is small, and although it connects with its fellow of the opposite side in the usual piscine manner, it is always in communication with a vein that issues from the cranial cavity through the foramen for the nervus vagus. There is in this fish no transverse pituitary canal such as is found in many of the *Selachii*.

Lateral to the several foramina above described, there is a large perforation of the suborbital shelf which transmits the ramus hyoideo-mandibularis facialis and the vena jugularis, and anterior to that foramen there is another perforation of the

* A small foramen is, by error, shown in figure 3, Plate II., lying slightly ventral to this large foramen. It does not exist in the fish.

shelf which transmits the arteria carotis externa and the ramus palatinus facialis, these two foramina being persisting remnants of the palatoquadrate fissure of Dean's (1906, p. 108) descriptions of embryos. That fissure of embryos lies, as shown in Dean's figures, between the palatoquadrate, the trabecula, and the anterior edge of a shelf of cartilage that projects laterally from the neurocranium beneath the hind end of the orbit and is fused, in its antero-lateral portion, with the palatoquadrate. The vena jugularis accordingly lies definitely ventral to this laterally projecting shelf-like process of the neurocranium, and hence also morphologically ventral and internal to the dorso-posterior portion of the palatoquadrate. If then this shelf-like process is an outgrowth of the neurocranium, the dorso-posterior end of the palatoquadrate, as shown by Dean, must be the processus oticus of that cartilage, but it seems much more probable that the shelf itself is the processus oticus, or extrabranchial element of the arch. Dean (*l. c.* p. 129) considers this shelf to be the posterior portion of the pharyngeal element of the mandibular arch, but in that case this element of the arch has fused with the neurocranium dorsal to the vena jugularis, which would be in marked exception to the conditions found in all other fishes that I know of (Allis, 1915). It accordingly seems to me, as above stated, that this shelf must represent the extrabranchial of the arch, or processus oticus quadrati, apparently found only partially fused with the palatoquadrate in Dean's six-month embryo. The vena jugularis, ramus hyoideomandibularis facialis, and arteria carotis externa would then all lie ventral and internal to this element of the arch, as they normally should, and the foramina for these several structures would represent the trigemino-facialis chamber of the fish, as I have already suggested in an earlier work (Allis, 1914).

The orbit has postorbital and antorbital processes. The postorbital process is a pronounced and slightly curved ridge which is fused ventrally with the suborbital shelf. The dorso-lateral antorbital process is a short but tall ridge which lies at the dorso-anterior edge of the orbit, and its base is perforated by a foramen which transmits the ramus ophthalmicus superficialis trigemini from the orbit to the ethmoidal canal. Immediately ventral to this process there is a foramen which transmits a vein and artery, and antero-ventral to this latter foramen there is another foramen which transmits the nervus ophthalmicus profundus; both these foramina leading into the median ethmoidal canal. A small foramen dorsal to these foramina also leads into the ethmoidal canal and gives exit to a small branch of the ophthalmicus superficialis. A small foramen on the dorso-mesial surface of the nasal capsule gives passage to a branch of the orbital branch of the external carotid, and anterior to it there is another small foramen for a delicate branch of the ophthalmicus nerve. The ventro-lateral antorbital process is simply a ridge which traverses the suborbital shelf and is continued onto the palatoquadrate, where it turns

posteriorly and joins the ventral end of the postorbital process, this ridge forming the boundary between the horizontal portion of the suborbital shelf and its ventrally projecting eaves-like lateral edge. Between its dorso-lateral and ventro-lateral processes the remainder of the antorbital process is a wide and gently rounded surface which extends from the orbit to the nasal capsule, and is so completely fused ventrally with the dorsal edge of the palatoquadrate that even the line separating the two cartilages cannot be recognised.

The suborbital shelf is a wide thin plate of cartilage which extends between the antorbital and postorbital processes, and has a narrow, ventrally projecting, eaves-like lateral edge, just above referred to. The shelf is prolonged posteriorly beyond the postorbital process, this postorbital portion of the shelf projecting ventro-posteriorly at a slight angle to the orbital portion, and apparently representing, as just above explained, the processus oticus quadrati. It gives origin, on its ventral surface, to the musculus protractor arcuum branchialium of Vetter's (1878) descriptions. On the ventral surface of the continuous shelf these two portions are separated from each other by a groove which lies directly ventral to the ventral end of the postorbital process and is directed postero-mesially. That part of the orbital portion of the shelf that lies lateral to the foramen for the nervus hyoideo-mandibularis facialis belongs to the palatoquadrate, and is probably formed by the epal (quadrate) and pharyngeal portions of the mandibular branchial bar, the pharyngeal element not projecting as a processus basilaris.

The cranial cavity has large anterior and posterior portions, separated by a narrow neck in the orbital region, this neck lying between the ventral edge of the zygous portion of the membranous interorbital wall and the summit of the rounded transverse presphenoid bolster. The posterior portion of the cavity is tall, with a concave anterior edge the dorsal end of which projects dorso-anteriorly above the orbit like the horn of a crescent. The postclinoid wall lies at about the middle of the length of this posterior portion of the cavity and projects anteriorly or antero-dorsally. Between it and the foramen magnum there is a depression in the cranial floor, and anterior to it, between it and the presphenoid bolster, is the large pituitary fossa. The postero-dorsal end of the hypophysial groove on the ventral surface of the basis cranii lies slightly posterior to the summit of the presphenoid bolster. A slight transverse ridge at about the posterior quarter of the pituitary fossa marks off a small posterior and deeper portion of the fossa. The foramina for the nervi facialis, trigeminus, and abducens lie dorsal or postero-dorsal to the postclinoid wall, and the small foramen for the pituitary vein antero-ventral to it.

The anterior portion of the cranial cavity increases gradually in height from its hind end up to the base of the median rostral

process, that point marking also the anterior end of the ethmoidal canal. This latter canal is large and is separated from the cranial cavity by cartilage slightly thinner than that of the basis cranii. Beyond the anterior end of the ethmoidal canal the cranial cavity contracts somewhat abruptly to its anterior end, that end being marked, on either side, by the foramen olfactorium. The cranial cavity of the adult accordingly shows, when compared with Dean's figures of embryos of this fish and with Schauinsland's figures of embryos of *Callorhynchus*, that the dorsal portion of the chondrocranium has undergone marked lateral compression in post-embryonic stages, the membranous mesial walls of the orbits being pressed together so that they meet and coalesce in the median plane in front of the midbrain and dorsal to the forebrain, a considerable portion of the cranial cavity of embryos thus being obliterated. Because of this, or correlated to it, the midbrain becomes, in the adult, widely separated from the hind end of the ethmoidal canal, and the forebrain is correspondingly elongated.

The two foramina olfactoria are separated from each other by a stout column of cartilage which lies nearly at right angles to the cranial floor, and each foramen is closed by a membranous cribriform plate. Each foramen opens directly into the mesial portion of the posterior end of the related nasal capsule, that capsule being directed antero-ventrally and bulging laterally so that it forms a pronounced swelling on the lateral surface of the chondrocranium. The ventral edge of the capsule reaches nearly, but not quite, to the ventral edge of this part of the chondrocranium, and the capsules of opposite sides are in contact in the median line, a septum nasi separating them from each other. This septum nasi is continuous, posteriorly, with the column of cartilage that separates the foramina olfactoria, that column lying in large part posterior to the plane of the foramina and representing the rostral stalk of embryos of *Callorhynchus* and of the Selachii. The septum nasi thus lies morphologically ventral to the stalk, and is formed either by a subethmoidal keel alone, or by that keel fused with the contiguous mesial sides of the nasal capsules, the rostral stalk forming the morphologically dorsal edge of the septum, as it also does in *Mustelus* (Gegenbaur, 1872, fig. 1, pl. 5) and *Scyllium* (Parker, 1876, fig. 4, pl. 37). The nasal capsules thus fuse with each other, in *Chimera*, ventral to the trabeculæ, as they do in the Selachii, this confirming the conclusion already arrived at that they have this position in *Callorhynchus*.

With the contact and fusion of the nasal capsules in the median line ventral to the trabeculæ, the ventro-lateral trabecular processes of opposite sides, if they existed in this fish, must also have been pressed together in the median plane, and their flaring ventral ends probably form some part of the beak-like prenasal process, that process being, as already stated, morphologically

subnasal, instead of prenasal in position. The palatine processes of the palatoquadrate must, however, also take some important part in the formation of this beak, for the anterior dental plates, which it supports, lying as they do posterior to the primary upper lips (Allis, 1917 *b*), must belong to the primary, or palatoquadrate dental arcade. These plates cannot accordingly be intermaxillary (premaxillary) teeth, as Schauinsland (1903, p. 14) suggests as possible in *Callorhynchus*, and they must be either vomerine or vomero-palatine teeth according as the term palatine is used to apply to teeth developed in relation to the palatine process of the palatoquadrate or in relation to some part of the palatoquadrate that lies posterior to that process. The posterior dental plate of either side would then be either a pterygoid or a palato-pterygoid plate, a pterygoid element quite certainly being included in it. Further facts in favour of considering the beak of *Chimera* to be formed in part by the palatine process of either side are:—

1. That the external surface of the prenasal beak gives articulation to the anterior end of a cartilage that is quite unquestionably an anterior upper labial, as will later be explained, and this anterior end of this labial is frequently, in the Selachii, in contact with the dorsal surface of the palatoquadrate but never in such contact with the neurocranium, as is also later explained.

2. That the beak of *Chimera* is traversed, on either side, by a small canal which, in the specimen used for illustration, begins on its dorsal surface by a single foramen and opens on its ventral surface by three small foramina which lie internal to the anterior dental plate. This canal is traversed by a branch of the nervus maxillaris trigemini which descends over the lateral edge of the nasal capsule and is evidently destined to innervate the anterior dental plate and the related tissues. The corresponding nerve in *Mustelus*, *Chamydoselachus*, and *Raia*, and hence probably in all of the Plagiostomi, runs forward along the external surface of the palatoquadrate and then over its ventro-lateral edge, thus being separated from the trabeculæ by the full width of the palatoquadrate, and while it might become enclosed in the lateral edge of the palatoquadrate it seems impossible that it could become so enclosed in the lateral edge of any cartilage of trabecular origin.

The mandibula presents no special features that seem to require consideration, but it may be mentioned that there are two surfaces for the articulation with the palatoquadrate, the antero-lateral one being an articular facet and the postero-mesial one an articular head. It is also to be noted that the line of the gape of the jaws, when the mouth is closed, is approximately parallel with the line of the trabeculæ, the plane of the epal and ceratal elements of the mandibular arch thus retaining its primitive perpendicular relations to the trabeculæ and hence being directed postero-ventrally instead of ventrally.

2. Nasal and Labial Cartilages.

The so-called nasal and labial cartilages of current descriptions of the Holocephali are much more numerous than the similarly named cartilages of the Selachii, and the conditions in the latter fishes must first be considered.

The nasal cartilages of the Selachii are limited to the ala nasalis (Nasenflügelknorpel), and this cartilage I have recently described in a certain number of these fishes and compared it with the cartilage in *Chimera* (Allis, 1917 *b*). It is accordingly not necessary to here consider it in the former fishes.

The labial cartilages of the Selachii are limited to one or two related to the upper jaw and one related to the lower jaw. Gegenbaur (1872) called the one or two former cartilages the anterior and posterior upper labials, and as he at that time considered the premaxillary and maxillary bones, respectively, of the Teleostei to be developed superficial to, and in relation to, these cartilages, he also called them the premaxillary and maxillary labials. These latter terms I shall avoid because of the implied homologies, which I consider not yet established. The single labial related to the lower jaw Gegenbaur called the lower, or premandibular labial, the latter term being used by him because he then considered this labial and the maxillary labial to together represent persisting remnants of a premandibular visceral arch. This latter term I shall also avoid, using in its place the indifferent term mandibular labial. If it should be later established that this labial and one or both of the upper labials are structures related to a premandibular arch or arches, they can then be given names that will show their relations to the arch or arches to which they belong.

The hind end of the mandibular labial and the corresponding end of one or both of the upper labials articulate with each other, or are connected by ligament, immediately posterior to the outer end of the line of the angle of the gape, and these ends of the labials there lie at a certain distance from the cartilages of the upper and lower jaws, separated from them by the thickness of the anterior edge of the musculus adductor mandibulæ. This point of articulation of the labials lies at a variable distance anterior to the quadrato-mandibular articulation, and it is shown in nearly all of Gegenbaur's figures of these fishes lying external to the mandibula.

In *Chlamydoselachus* there are two upper and one lower labials, and they have been described or figured by Goodey (1910), K. Fürbringer (1903), and Luther (1909 *a*). The anterior labial gives attachment, along the dorsal edge of its anterior end, to a ligament which has its origin on the anterior wall of the orbit at about the middle of its height. Numerous short ligamentous strings run from the antero-ventral edge of this ligament into the tissues of the upper lip, this seeming to indicate that the ligament has been differentiated from an extensive dermal or

subdermal fascia. The posterior upper labial lies internal and aboral to the anterior one and is closely attached to the musculus levator labii superioris, the tendon of that muscle passing ventral to the ligament related to the anterior labial and having its insertion on the ventro-lateral antorbital process.

In a specimen that I have of *Mustelus*, probably *vulgaris*, there are two upper labials, and they are strikingly similar to those shown by Gegenbaur in a figure (1872, fig. 3, pl. 11) said, in the explanations of the plates, to be of *Mustelus*, but referred to in the text as of *Galeus*. In this figure the jaws are furnished with sharp pointed teeth; and Marshall and Spencer (1881) and Ridewood (1895) have each independently called attention to the fact that, because of these teeth, the figure is probably of *Galeus*, as it is said by Gegenbaur to be in his text. But, curiously enough, in this figure with sharp teeth, and hence probably of *Galeus*, there are two upper labials similar to those I find in my specimen of *Mustelus*, identified by the presence of pavement teeth, while in the figure said by Gegenbaur (*l. c.* fig. 2, pl. 12) to be of *Galeus*, but furnished with pavement teeth and hence probably of *Mustelus*, there is but one labial. Gegenbaur furthermore says (*l. c.* p. 214) that both Meckel and J. Müller also found but one upper labial in *Mustelus*; but K. Fürbringer (1903) has since found two of them in *Mustelus equestris*. If these labials do not vary in different specimens or species of *Mustelus*, it is thus probable that Gegenbaur, in his figures above referred to, interchanged either the labials or the teeth, as well as the names, of the two fishes.

But, whatever the error in these two figures of Gegenbaur's may be, in my specimen, which has pavement teeth, there are two upper labial cartilages, and they both lie in the maxillary portion of the labial fold. The anterior labial is about twice as long and much stouter than the posterior one, and lies external and oral to it, as does the anterior labial in *Chlamydoselachus*. Its hind end lies but slightly anterior to the hind end of the posterior upper labial and is attached to that labial, but not to the mandibular one, by ligamentous tissues. The anterior half, approximately, of the anterior labial lies internal to the ventral edge of the musculus levator labii superioris, in a pocket formed in the tough connective tissues that cover the external surface of the palatoquadrate. The labial is freely movable in this pocket, and its anterior end lies directly upon the palatoquadrate, in a scarcely perceptible depression in that cartilage, but is in no way attached either to it or to the chondrocranium. The walls of the pocket are differentiations of a dermal or subdermal fascia which is somewhat ligamentous in character, and which extends antero-mesially and is attached to the posterior surface of the nasal capsule; this fascia doubtless representing the one from which the ligament attached to this labial in *Chlamydoselachus* is developed.

The posterior upper labial of *Mustelus* is bound by ligamentous

tissues to the mandibular labial, and can thus be said to articulate with it. From near its hind end a ligamentous strand runs antero-dorsally and joins a stouter ligament which arises from the median transverse aponeurosis of the musculus adductor mandibulae, at the inner end of the line of the angle of the gape. The ligament so formed is joined by a ligamentous slip from about the middle of the anterior labial, and then joins and fuses in part with the internal surface of the dorsal, maxillary portion of the adductor muscle and in part with the closely related musculus levator labii superioris. A part of the ligament continues forward and is inserted on the posterior surface of the nasal capsule at the lateral edge of the large surface of insertion, on that capsule, of a part of the musculus levator labii superioris. There are thus, in this fish, two ligamentous structures connecting the upper labials with the nasal capsule. In *Chlamydoselachus* this connection is, as just above stated, with the antorbital wall.

In *Triakis fasciatum* there are two upper labials, and they closely resemble, in relative size and arrangement, those in *Mustelus*. The hind ends of the two labials lie close together, and both are bound by ligamentous tissues to the hind end of the mandibular labial, but the posterior upper labial alone articulates with that labial. The anterior end of the anterior upper labial rests directly upon the external surface of the palatoquadrate, as in *Mustelus*, but it is not enclosed in a pocket of the connective tissues of the region. A broad stout ligamentous band arises from the external surface of the palatoquadrate, at its oral edge and slightly anterior to the angle of the gape, and running antero-mesially across the external surface of the anterior upper labial is inserted on the internal surface of the nasal latero-sensory canal, close to the postero-mesial edge of the nasal capsule.

In two small specimens of *Scyllium canicula* I find, as Gegenbaur did, but one labial, and it quite certainly corresponds to the anterior upper labial of *Mustelus*, as Gegenbaur concluded. It extends forward along the ventral edge of, or slightly internal to, the musculus levator labii superioris, and its anterior end lies, as does that of the anterior upper labial of *Mustelus*, directly upon the external surface of the palatoquadrate, in a slight depression in that cartilage, but it is not enclosed in a pocket of connective tissue. This end of the labial lies directly internal to the posterior portions of the nasal and rostral sections of the latero-sensory canals. In one of the two specimens, but not in the other, the mandibular labial hooked around the angle of the gape, as Luther (1909 *a*) shows it in his figure of *Chiloscyllium*, this suggesting the possible fusion of a much reduced posterior upper labial with the mandibular labial.

The anterior end of the anterior upper labial is thus, in each of these few Selachii, either in contact with or closely related to

the dorsal surface of the palatoquadrate, and it is also either attached to, or related to, ligamentous or fibrous tissues which are attached to the chondocranium in the nasal region; and these are probably universal conditions in these fishes.

In *Chimara* Hubrecht (1877) describes five cartilages that are called by him nasal cartilages, and four that are called labials, the nasal cartilages being designated by the letters *f*, *g*, *k*, *l*, *m*, and the labial cartilages by the letters *a*, *c*, *d*, *e*. The letter *n* is used by Hubrecht to designate a process of the cartilage *k*, this cartilage accordingly sometimes being referred to as the cartilage *kn*.

The cartilage *k*, with its large process *n*, is called by Hubrecht the Nasenmuschel, and as it certainly represents some part of the ala nasalis of the Plagiostomi, it may be referred to as that cartilage. It encircles the antero-mesial or so-called ingress nasal aperture, and I have recently fully described it in this fish (Allis, 1917 *b*).

The cartilage *l*, shown in figure 4 (Pl. II.), is a small and irregular plate of cartilage which lies in the mucous tissues along the lateral edge of the process *n* of the ala nasalis, and it extends from that process to the inner surface of the cartilage *fy*. It bounds the dorso-mesial edge of the postero-lateral nasal aperture, and is attached both to the process *n* and the cartilage *fy* by connective or fibrous tissues, its point of attachment to the latter cartilage lying immediately beyond the base of the nasal-fold process of that cartilage, to be described immediately below.

The cartilage *m* is a thin, flat, curved, triangular cartilage which is attached by its pointed mesial end to the dorso-mesial surface of the ala nasalis (cartilage *kn*) near its external edge, and from there extends ventro-latero-posteriorly in the nasal portion of the naso-labial fold. A small nodule of cartilage may be found attached to its latero-posterior edge.

The cartilages *f* and *g*, said by Hubrecht to be found separate in *Callorhynchus*, are fused in *Chimara*, to form a single piece called by Hubrecht both a Lippenknorpelträger and a Nasenflügelknorpel. The two parts *f* and *g* differ slightly in coloration and appearance, suggesting that they are of independent origin, the part *g* being a flat plate-like superficial cartilage, and the part *f* a stout rounded and curved rod, which arises from the ventro-posterior end of the plate-like portion of the cartilage and may be called the pedicel of the entire cartilage. The plate-like portion of the cartilage lies, in the posterior half of its length, in a nearly horizontal position along the outer edge of the nasal capsule. Its dorso-anterior half turns dorso-anteriorly across the outer edge of the nasal capsule, and there lies on the outer surface of that capsule, passing latero-posterior to the lateral rostral process and being strongly but flexibly attached to that process by ligamentous tissues. Approximately at the point where the process turns dorso anteriorly, there is a prominent eminence on its internal

surface, and this eminence rests upon the little eminence on the dorsal surface of the ala nasalis (cartilage *kn*) that is described in my earlier work (Allis, 1917 *b*), the two cartilages there being strongly but flexibly attached to each other by connective or ligamentous tissues. The pedicel of the cartilage turns sharply mesially, in a rounded angle, and passing through a notch in the postero-ventro-lateral edge of the nasal capsule runs along the postero-lateral edge of the postero-lateral nasal aperture and reaches a small perforation of the chondrocranium that lies immediately ventral to the ventro-posterior edge of the fenestra nasalis. This perforation of the chondrocranium is filled with ligamentous tissues, and to these tissues the foot of the pedicel is strongly but flexibly attached, the position of this pedicel strongly resembling that of the anterior upper labial in *Heterodontus* (Allis, 1917 *b*).

On the ventral edge of the cartilage *fy*, at about the posterior third of the length of its plate-like portion, there is a slender curved process which projects ventrally into a ridge on the internal surface of the nasal portion of the naso-labial fold, this ridge quite certainly representing the tissues that enclose the process β of the ala nasalis of the Plagiostomi (Allis, 1917 *b*). Because of its position, this process of the cartilage *fy* may be called the nasal-fold process. It is thinner than the body of the cartilage *fy*, is flexible, and in many instances seems to be a primarily independent piece of cartilage that has secondarily and not completely fused with the cartilage *fy*. In several instances there was a foramen between the base of this process and the body of the cartilage, this foramen giving passage to a delicate nerve which was apparently a branch of the nervus maxillaris trigemini. In other specimens this nerve passed between the process and a crescentic cartilage described immediately below. The cartilage *l* is attached to the inner surface of the cartilage *fy* immediately beyond the base of this nasal-fold process.

In the hollow of the curve formed by the posterior edge of the nasal-fold process of the cartilage *fy* and the ventro-posterior portion of the body of that cartilage, lies the crescentic piece of cartilage just above referred to. This cartilage is of the same consistence as the nasal-fold process, and lies, as that process does, in the ridge on the internal surface of the naso-labial fold, and it is apparently the cartilage *e* of Hubrecht's descriptions of *Chimera monstrosa*. Both it and the nasal-fold process of the cartilage *fy* are shown in one of Luther's figures of the latter fish (1909 *b*, p. 37), and K. Fürbringer (1903) also refers to both of them, the two together being considered by him to represent the cartilage *e* of Hubrecht's descriptions. In *Chimera colliei* the crescentic cartilage is connected with the cartilage *d*, which I consider to be the posterior upper labial, by a band of tough fibrous tissue which passes across the external surface of the cartilage *fy*, a slip of the tissues being sent antero-

dorsally along the external surface of the latter cartilage. This crescentic cartilage and the nasal-fold process of the cartilage *fy* thus seem to both be chondrifications of this fibrous tissue, one of them related to the cartilage *d* (posterior upper labial) and the other to the cartilage *fy*.

The cartilage *fy* is thus a strongly curved cartilage which encircles the lateral half of the fenestra nasalis, lying against the external, and not the internal, surface of the edge of the fenestra, and it either sends a process into the ridge on the internal surface of the naso-labial fold, or becomes secondarily fused with a cartilage that is developed independently in that ridge. The lining membrane of the nasal capsule is not attached to this cartilage *fy*, as it is to the cartilage *kn* (ala nasalis), lying wholly internal to it. The cartilage is capable of a swinging, dorso-ventral motion around a line passing through its two points of attachment to the chondrocranium, the cartilage passing backward and forward across the outer, and not the inner, surface of the lateral edge of the fenestra nasalis. The posterior one of these two motions is impressed upon it by the musculus levator anguli oris anterior of Vetter's (1878) descriptions, acting both through its own tendon and the long and slender ligament called by Luther (1909 *b*) the levator cartilagineus praelabialis, the contrary motion apparently being caused in part by the simple elasticity of the parts, and in part by the action of the musculus labialis posterior. The musculus labialis anterior, which is attached by one end to the dorso-anterior end of this cartilage and by the other to the cartilage *d* (posterior upper labial), would seem to exert its action on the latter rather than on the former cartilage.

Hubrecht says that the process α of Gegenbaur's descriptions of the Selachii, together with that part of the edge of the nasal capsule that, in those fishes, bounds the mesial edge of the postero-mesial nasal aperture, corresponds to the cartilage *kn* of *Chimera*, this latter cartilage thus being considered by him to be cut off from the outer edge of the nasal capsule, and its process *n* to correspond to the process α of the Selachii. The cartilage *fy* of *Chimera* is said to correspond to the process β of Gegenbaur's descriptions of the Selachii, the cartilage *e* of *Chimera* to represent the anterior upper labial of the Selachii, and the cartilage *l* to be a remnant of that part of the ala nasalis that primarily connected the cartilages *kn* and *fy*.

Both Fürbringer (1903) and Luther (1909 *b*) apparently accept Hubrecht's conclusions regarding the homologies of these several cartilages of *Chimera*; but Luther nevertheless calls the cartilage *fy* a premaxillary cartilage, which must mean that he considers it to be a labial and not a Nasenflügelknorpel, and he neither mentions, nor shows in his figures, the cartilage *e*. Vetter (1878), who knew of Hubrecht's work only by title, describes as a premaxillary cartilage a cartilage that must be the cartilage *fy* of Hubrecht's descriptions, but he makes no

mention of the cartilage *e*. He shows, in one of his figures, a so-called Nasenflügelknorpel, which is said to be longer than the premaxillary cartilage, to lie directly mesial to it, and to be derived from the nasal capsule. This cartilage, as shown in Vetter's figure, is not found in *Chimera colliei*, and it is not shown in Hubrecht's figures of *Chimera monstrosa*. Its dorsal end corresponds, in position, to the lateral rostral process of these fishes, the remainder of it apparently being the cartilage *m* of Hubrecht's descriptions, or both that cartilage and the cartilage *kn*.

My conclusions regarding the homologies of these several cartilages differ somewhat from those of these several authors, and they are based on my interpretation of the lips and nasal apertures of this fish as set forth in the work already several times referred to as now in press (Allis, 1917 *b*), and which should here be consulted.

In the Plagiostomi it is always that part of the ala nasalis that encircles the antero lateral and ingress nasal aperture that is the most developed, the part that encircles the postero-mesial and egress aperture always being less developed and in some cases wholly wanting. In *Chimera*, on the contrary, it is the part of this cartilage that encircles the antero-mesial and here so-called ingress aperture that is the most developed, that part of the cartilage that encircles the antero-lateral and originally ingress aperture having undergone marked reduction. That part of the cartilage that encircles the antero-mesial aperture is represented in the cartilage *kn* of Hubrecht's descriptions, the cartilage *k* representing that part of the ala nasalis of the Plagiostomi that lies mesial to and between the processes ξ and β of Gegenbaur's (1872) descriptions of the latter fishes, and the process *n* of the cartilage *k* representing the process α of the Plagiostomi together with the process that Gegenbaur calls, in *Mustelus*, the process α' . The process β of the Plagiostomi is represented in *Chimera* in the little crescentic cartilage that lies in the ridge on the internal surface of the naso-labial fold, and a remnant of that part of the ala nasalis that originally lay between this process and the process α is represented in the cartilage *l* of *Chimera*.

The cartilages *m* and *g* of *Chimera* have no homologues in the Plagiostomi, but they, the nasal-fold process of the cartilage *g*, and the little adjacent crescentic cartilage are all evidently of fibrous origin and all quite certainly chondrifications of a subepidermal layer of fibrous tissue. Just what this layer of tissue is I have been unable as yet to definitely determine, but it would seem to be the fibrous layer of the corium. The nasal-flap cartilage of my descriptions of *Raia* (Allis, 1916) is certainly a chondrification of this same layer of tissue, and as the process α of the ala nasalis of that fish has exactly the same subepidermal position as the nasal-flap cartilage, that process must also be of fibrous origin. But, if this process α is of fibrous origin, the alar ring, of which it is a process, must also be of similar origin, all

of these cartilages then being chondrifications of a single layer of subepidermal fibrous tissue. This fibrous layer certainly passed, originally, beneath the epidermal tissues that were modified to form the sensory epithelium of the nasal pit, and when this sensory tissue was invaginated to form that pit, the fibrous layer must have been invaginated with it. The nasal capsule might then itself also be a chondrification of this same layer of fibrous tissue, and hence not a part of the axial skeleton, as it is usually considered to be; and its development in the Plagiostomi is decidedly in favour of this assumption.

The cartilage *f* of Hubrecht's descriptions of *Chimera*, although it lies along the edge of the postero-lateral nasal aperture, has no relations whatever to the original antero-lateral nasal aperture, and hence is not a derivative of the ala nasalis, and its position strongly indicates that it is an anterior upper labial. It has approximately the position of that labial in *Heterodontus*, and also that of the single labial of *Ceratodus* (Allis, 1917 *b*), and the fact that its anterior end is in contact with a part of the chondrocranium that is quite unquestionably derived from the palato-quadrate is in accord with the conditions that I have above described in several of the Selachii, and would be wholly exceptional for a cartilage derived from the ala nasalis. If, in one of the Selachii above referred to, the fibrous or ligamentous tissues that are related to the anterior upper labial, and that are attached to the chondrocranium in the nasal region, were to undergo chondrification, a cartilage would arise that would closely resemble the cartilage *fg* of *Chimera*, one part of this cartilage thus being of labial origin and the other of independent fibrous origin. Furthermore, this origin of the cartilage is in accord with its relations to the terminal branches of the nervus maxillaris trigemini, for the more important terminal branches of that nerve pass internal to the cartilage, between it and the nasal capsule, which is not their relations either to any part of the nasal capsule of the Selachii or to the ala nasalis of those fishes, but is their relations to the anterior upper labial and its related ligaments in those fishes. What is apparently the cartilage *f* in Schauinsland's descriptions of embryos of *Callorhynchus* (1903, *n*², fig. 127) has, however, decidedly the appearance of being a part of the ala nasalis, but the cartilages as there shown are so different from those in the adult *Chimera* that I am unable to make any comparison. Two of the cartilages described by Schauinsland, called by him the cartilages *l*¹ and *l*², are said by him to lie in mucous folds "welche die Schnauze umgeben" and to represent preoral visceral arches. Premandibular arches they may represent, as may also the labial cartilages of the Selachii, but they certainly cannot represent preoral arches.

The cartilages *c* and *d* of Hubrecht's descriptions were considered by him to together represent the posterior upper labial of the Selachii. They are first said by him to be separate and

distinct cartilages, capable of a slight motion with each other, but they are later said to be so completely fused that there is even but slight persisting indication of the line of separation between them. Vetter found them as separate cartilages and considered them to be, respectively, the maxillary and mandibular labials. K. Fürbringer found them more independent of each other than they are said to be by Hubrecht, but less so than described and figured by Vetter, and he agrees with Hubrecht in considering them, together, to represent the posterior upper labial. Luther shows them as a single cartilage, and they together form the maxillary, and hence posterior upper labial of his descriptions. I find them as separate and distinct cartilages lying immediately posterior to the angle of the supplementary secondary gape of the mouth and straddling the line prolonged of that angle, that angle lying near the inner end of the line of the angle of the gape, as fully described in my work now in press (Allis, 1917 *b*). One of these cartilages thus lies dorsal and the other ventral to the line of the angle of the gape, in the positions respectively of the posterior upper and mandibular labials of the *Selachii*, and I accordingly consider them, as Vetter did, to represent, respectively, those labials, notwithstanding that they both, and particularly the posterior upper labial, seem to be chondrifications of the same fibrous layer that has given origin to the cartilages *g*, *m*, and *e* of Hubrecht's descriptions.

The posterior upper labial, thus identified, is a small and somewhat rectangular cartilage that lies immediately dorsal (morphologically posterior) to the ventro-posterior-lateral end of the plate-like portion of the cartilage *fy*. It is strongly but loosely attached, by its ventral (morphologically anterior) end, to the latter cartilage, and also strongly but quite rigidly attached, by the adjoining, posterior (morphologically ventral) edge, to the dorsal end of the mandibular labial. This latter attachment allows of but little motion between the two pieces, such little motion as there is being latero-mesial. The labial gives insertion, on its dorsal (morphologically posterior) edge, to the *musculus levator anguli oris anterior*, and either on its external surface or its anterior (morphologically dorsal) edge, to the *musculus labialis anterior*, the other end of the latter muscle being inserted on the dorso-anterior end of the cartilage *fy*.

The mandibular labial (cartilage *e*) is a stout bar of cartilage with a large triangular process on its anterior edge near its ventral end. The anterior edge of its dorsal end is strongly attached to the posterior upper labial, as just above described. Its ventral end lies in the hind end of the labial part of the naso-labial fold. Its anterior process passes internal to the hind end of the supra-mandibular furrow, and lies in supporting relations to the supplementary secondary lower lip, this process and the nasal-flap process of the cartilage *g*, together with the related crescentic cartilage above described, thus being opposed to each other in

these supplementary secondary lower and upper lips. The anterior end of the anterior process of the mandibular labial gives insertion to a tendon of the musculus levator anguli oris posterior, that tendon passing downward across the internal surface of the labial to reach its point of insertion, as shown in Luther's figure of *Chimæra monstrosa*. Connected with this tendon, and as direct ventral continuations of it, there are two small ligaments, one of which joins the ligament *l* of Luther's descriptions, to be described immediately below, while the other runs ventromesially along the external surface of the mandibula, internal to the musculus labialis posterior, and has its insertion in tough fibrous tissues in the median line. The tendon of the musculus labialis posterior runs dorsally along the internal surface of the mandibular labial, internal (mesial) to the tendon of the musculus levator anguli oris posterior, and has its insertion on the internal surface of the mandibular labial near its dorsal end, this also being as shown in Luther's figures of *Chimæra monstrosa*.

The cartilage *a* of Hubrecht's descriptions was considered by him to be, together with a related "Bandapparat," the homologue of the mandibular labial of the Selachii. Vetter does not mention this cartilage. K. Fürbringer accepts Hubrecht's statements regarding it as correct. Luther considers this cartilage, alone, to be the homologue of the mandibular labial of the Selachii, and, following Gegenbaur's nomenclature, he calls it the pre-mandibular labial. The Bandapparat he considers to be an independent and superficial structure, and he fully describes it in *Chimæra monstrosa*.

In *Chimæra colliei*, the thick lower lip contains a mass of dense tough fibrous tissue which extends the full length of the lip and from its oral edge a certain distance posteriorly. This mass of tissue completely surrounds the musculus labialis posterior, that muscle traversing a canal-like perforation of the posterior portion of the tissue without being in any way attached to it excepting only at its origin near the symphysis of the mandibles. The anterior (oral) end of the cartilage *a* is strongly attached to this tough fibrous tissue, and it abuts against the posterior surface of the musculus labialis posterior, the cartilage being grooved to receive the muscle and the edges of the groove sometimes projecting to such an extent that the cartilage is decidedly Y-shaped. External to the symphyseal edge of the cartilage, and strongly attached to it, there is a small piece of strongly calcified cartilage which is grooved on its external surface to lodge a section of the mandibular latero-sensory canal. On its symphyseal edge the cartilage *a* gives origin to ligamentous tissues which cross the median line and are attached to the corresponding cartilage of the opposite side, this apparently being as shown in Luther's figure of *Chimæra monstrosa*, but the musculus labialis inferior of that author's descriptions of *Chimæra monstrosa* is not found in my specimens of *Chimæra colliei*.

The ligament *l* of Luther's descriptions (1909 *b*, fig. 28) is

found in my specimens of *Chimera collicii* arising from the tough fibrous tissues that cover the ventral surface of the symphysis of the mandibles, and also from the external surface of the cartilage *a*. Running latero-posteriorly in a curved line, this ligament is joined first by a ligament coming from the median line posterior to the cartilage *a*, and then by a ligament coming from the ventral edge of the mandibular labial and to which reference has just above been made. The ligament so formed runs posteriorly across the postero-ventral edge of the mandibula, in a slight groove in that edge, and then runs upward along the internal surface first of the mandibula and then of the palato-quadrato, and is inserted on a little cartilage which seems to correspond to the spiracular cartilage of Hubrecht's descriptions of *Chimera monstrosa*, notwithstanding that it lies much farther from the hind edge of the mandibula. This little cartilage is probably a persisting remnant of a mandibular branchial ray such as is frequently found in the Selachii and there currently called a spiracular cartilage, but it cannot be the homologue of the spiracular cartilage of the Batoidei, that cartilage being the extrabranchial, or suprapharyngobranchial, of the mandibular arch and being represented, in *Chimera*, in the processus oticus quadrati, as already stated. The ligament related to this little cartilage may then represent either certain persisting fibrous tissues of the mandibular arch, or be a ligament derived from certain fibres of the primitive constrictor of the arch such as are found in *Astrape* (Luther, 1909 *a*, p. 14), and to which I have made reference in a work now in press on the homologies of the muscles related to the visceral arches in the gnathostome fishes (Allis, 1917 *a*). If this little cartilage be a persisting remnant of a mandibular branchial ray, then the cartilage *a* would also seem to be such a remnant. Luther (*l. c.* p. 46) considers the cartilage *a* to be a chondrification of the membrane in which it lies.

3. Rostral Processes.

The three rostral processes of the adults of all of the Chimæroids are said by Garman (1904) to be attached to the chondrocranium by ligaments "in such a way as to admit of considerable movement of their distal extremities up and down," the evident inference being that Garman did not find, in any of these fishes, the cartilage of these processes continuous with that of the chondrocranium. Hubrecht, however, shows all three of these processes directly continuous with the cartilage of the chondrocranium, and he suggests that the median process may be the homologue of the rostral process of the Selachii, and that the lateral processes are probably represented, in the latter fishes, by ligaments. Schauinsland (1903) refers to these processes, in embryos of *Callorhynchus*, as "mit dem Schädel fest verbundenen Knorpeln," and in his figures he shows all three of them as outgrowths of the septal cartilage of his descriptions

and as directly continuous with it, the processes thus being of trabecular origin. Schauinsland says that these processes support the rostrum. Garman (1904, p. 252) says there is no rostrum in these fishes, but the presence of the rostral processes suggests that a rostrum existed in ancestral forms and has become obsolete. Gegenbaur (1898) says that the three rostral processes correspond to, but are not directly descended from, the three-limbed rostral basket of the Carchariidæ and Scylliidæ, this implying that they are directly continuous with the cartilage of the chondrocranium. Dean (1906) shows the median process directly continuous with the cranial cartilage in a six-month embryo of *Chimæra colliei*, but says (*l. c.* p. 129) that: "I am inclined to interpret it as an element, *i. e.*, a fin support, transposed from a hinder position," which would mean that it was not primarily a part of the cranial cartilage. The lateral rostral processes he says are "later developed into long and separately jointed elements." He considers the median bar of the rostral basket of the Carchariidæ and Scylliidæ to be probably represented in the septal plate of Schauinsland's descriptions of *Callorhynchus*, and hence not in the median rostral process of that author's descriptions. The lateral bars of the rostral basket of the Selachii are said to be possibly the homologues of the little processes *s* of Schauinsland's descriptions of *Callorhynchus*, to be later considered.

In my specimens of *Chimæra colliei*, I find the median rostral process articulating with and strongly bound by ligamentous tissue to, but not directly continuous with, a slight eminence of the chondrocranium that lies on its dorsal surface between the two anterior openings of the ethmoidal canal. The lateral process of either side arises from a thin and flexible portion of the anterior edge of the dorsal wall of the nasal capsule, and it is apparently directly continuous with the cartilage of that wall, the surfaces, when the process is removed, always appearing fractured. The median process runs at first dorso-anteriorly and then turns somewhat abruptly ventro-anteriorly, and extends approximately to the level of the outer ends of the lateral processes. From about the middle of the length of the proximal portion of the median process a ligament arises and runs antero-ventrally in the median line until it reaches the level of the lateral processes. There it spreads dorsally, ventrally and laterally and is lost in a layer of tough fibrous tissue that lies internal to the latero-sensory canals on the ventro-anterior surface of the snout, and forms part of the fibrous layer of the corium, to be later described in connection with the ampullary tubules. A stout ligament, which extends mesially from the outer end of each of the lateral processes, also lies in this tough tissue, and is thus indirectly connected with the median ligament just above described as well as with its fellow of the opposite side. Gegenbaur (1898) found these three ligaments represented by cartilage in one specimen of *Chimæra*, the ligaments of my specimen thus being capable of

undergoing chondrification. The presence of these three ligaments connecting the three rostral processes of *Chimera*, and their possible chondrification, thus suggest that they and the processes together represent a rostral basket similar to that found in the Carchariidae and Scylliidae, but everted. In certain specimens of *Mustelus* I find similar ligamentous or fibrous strands connecting the median and lateral limbs of the rostral basket, and if such a basket were to be everted, by the lateral limbs passing antero-ventrally external to the median limb, the conditions found in *Chimera* would apparently arise; the lateral processes of *Chimera* thus representing the basal portions of the lateral limbs of the basket of the Selachii, those portions of those limbs being attached to the nasal capsules as are the processes in my specimens of *Chimera*.

Garman says that, in *Chimera monstrosa*, the median rostral process "presents the appearance of having originally been attached near the nasal capsule, as in *Callorhynchus*, and of having the basal portion, for a short distance, brought back against and fused with the frontal region of the skull." This is certainly also the appearance presented by the process in *Chimera colliei*; but it is probable that this apparent folding backward of this process is due to the marked antero-ventral growth of the anterior portion of the naso-ethmoidal cartilage, the rostral stalk being carried forward beyond the base of the median rostral process. Comparison of Schauinsland's figure 125 of *Callorhynchus*, giving a median vertical sectional view of an embryo of *Callorhynchus*, with the accompanying figure 2 (Pl. I.), giving a similar view of the adult *Chimera colliei*, will show that this must be so. Comparison with Sewertzoff's figures of embryos of *Pristiurus*, and with Dean's figures of embryos of *Chimera colliei*, then further shows that, because of the antero-ventral growth of this part of the chondrocranium, the antero-ventral half of the fenestra præcerebralis has been carried forward on either side of the median rostral process, that the edges of the fenestra anterior to the process have then fused with each other, and that posterior to the rostral process the fenestra has been closed by lateral compression of the cranium, the ethmoidal canals of opposite sides coalescing in the median line and their floors forming the roof of the cranial cavity and their roofs a secondary roof to the cranium. The fenestra præcerebralis is thus completely closed in the adult *Chimera*, but in embryos of *Callorhynchus* a part of it still persists as the opening *t* of Schauinsland's figures.

A stout ligament arises from the dorsal surface of the chondrocranium at the posterior edge of the nasal capsule, there lying postero-lateral to the corresponding lateral rostral process. This ligament lies at first at right angles to the chondrocranium, and as it is stout and stiff, it looks like a short ligamentous horn which extends to the internal surface of the fibrous layer of the corium above referred to as being related to the tubules of the ampullary organs and to be described immediately below. There

the ligament breaks up into numerous branches which spread in every direction along the internal surface of the fibrous membrane. From the anterior surface of the columnar portion of the ligament a branch ligament is sent antero-ventrally beneath the fibrous membrane. The little cartilaginous eminence *s*, shown in Schauinsland's figures of *Callorhynchus* on the dorsal surface of each nasal capsule, corresponds approximately, in position, to this ligament of *Chimera*.

4. Ampullæ.

The ampullæ were examined in two specimens. In one of these specimens there were five large occipital ampullary pores lying in line along the anterior edge of that portion of the supratemporal commissure (lateral canal, Cole, 1896) of the latero-sensory canals that lies between the posterior ends of the supraorbital and infraorbital canals. The tubules that start from these pores immediately penetrate a subepidermal membrane which extends over nearly the entire surface of the head, and, lying in that membrane, between external and internal layers of it, run forward dorsal to the orbit and terminate in a group of five ampullæ that lie immediately dorso-lateral to the median rostral process, these ampullæ also lying between the two layers of the subepidermal membrane. Dorso-anterior to the eyeball, between it and the supraorbital latero-sensory canal, there is a group of twelve supraorbital pores, the tubules from which also penetrate the subepidermal membrane and, running antero-ventrally, terminate in an equal number of ampullæ that lie ventral to the ampullæ of the occipital pores and, like them, between the two layers of the subepidermal membrane. Anterior to these supraorbital pores, in the anterior end of the space enclosed between the supraorbital and suborbital latero-sensory canals, there are three groups of pores more or less contiguous one with the other. In the two dorsal groups together there were thirty pores, and in the ventral group twelve pores. The tubules from the two dorsal groups penetrate the subepidermal membrane, and running dorsally, dorso-posteriorly or posteriorly, terminate in ampullæ that lie between the two layers of the subepidermal membrane, close to the ampullæ of the supraorbital pores. The tubules of the ventral group perforate first the outer and then the inner layer of the subepidermal membrane and terminate in ampullæ that lie close against the internal surface of that membrane, in the region between the dorsal and lateral rostral processes. Ventral to this latter group of pores there are numerous pores, many of them minute, covering that portion of the ventro-lateral surface of the snout that lies between the suborbital latero-sensory canal and the supramaxillary fold, and antero-mesial to the point where the supraorbital canal joins the outer buccalis canal. The tubules leading from these pores all run dorsally between the two layers

of the subepidermal membrane, and apparently all perforate the inner layer of that membrane and terminate in ampullæ that lie internal to it, in the region between the dorsal and lateral rostral processes. The tissues were, however, here so dense and tough that the relations of all of these ampullæ to the membrane could not be definitely determined.

The ampullæ above described are all innervated by branches of the ramus ophthalmicus superficialis trigemini, these branches being all given off after that nerve issues from the ethmoidal canal through its anterior opening, the branches destined to the ampullæ that lie between the two layers of the subepidermal membrane all perforating the inner layer of that membrane to reach the ampullæ. These ampullæ correspond, in position, to the larger one of the two supraorbital groups of Cole's (1896) descriptions of *Chimera monstrosa*, the smaller group of supraorbital pores of that author's descriptions having approximately the position, in *Chimera colliei*, of a group of ampullæ that are innervated by the nervus buccalis.

Cole says (1896, p. 655) that the ramus oticus facialis supplies "the most ventral of the ampullæ opening on the surface by the large occipital pores." No such branches of the ramus oticus could be found in my specimens of *Chimera colliei*, and as the ampullæ related to these occipital pores all lie on the dorsal surface of the snout, at a great distance not only from the related pores but also from the branches of the oticus shown in Cole's figure, this would seem to be an error.

The buccalis ampullæ are found in three groups, two innervated by the inner buccal nerve of Cole's descriptions and one by the outer buccal. The dorsal group of inner buccalis ampullæ lies on the dorsal surface of the snout, internal to, or slightly posterior to, the occipital and supraorbital groups of ophthalmicus ampullæ, and, like those ampullæ, between the two layers of the subepidermal membrane, these ampullæ having approximately the position of the posterior group of supraorbital ampullæ of Cole's descriptions. The tubules of these ampullæ run postero-ventrally, internal to the ophthalmicus ampullæ and tubules and between the two layers of the subepidermal membrane, and with one exception they all open on the external surface in the space included between the latero-sensory canals innervated by the inner and outer buccalis nerves of Cole's descriptions, the former canal being the one to which I have above referred as the suborbital canal. Nine of these pores form a sub-group which lies in the dorso-posterior corner of that space, while one of them opens somewhat ventro-anterior to that sub-group; and associated with the tubules of these pores there is the one exceptional tubule, which opens by an isolated pore that lies posterior to the posterior hyomandibular latero-sensory canal of Cole's descriptions. A second sub-group, of seven large pores, lies immediately ventral to the inner buccalis suborbital canal, in a large bend at about the middle of its length, and a

third sub-group, of ten pores, dorsal to the outer buccalis canal and postero-lateral to the point where that canal is joined by the supraorbital canal.

The second, or ventral group of inner buccalis ampullæ has the position of the group B² of Cole's descriptions, and it also lies between the two layers of the subepidermal membrane, about midway between the median and lateral rostral processes. From there the tubules run postero-ventrally, internal to the tubules of the dorsal buccalis ampullæ, and open on the external surface in a long line which begins at the point where the outer buccalis canal falls into the anterior one of the two-hyomandibular canals of Cole's descriptions and extends along the dorso-anterior edge of the latter canal until it reaches the postero-ventral end of the supramaxillary fold. There the line of the ampullary pores turns dorso-anteriorly along the edge of the supramaxillary fold, and so continues nearly to the median line.

The outer group of buccalis ampullæ is Cole's group B¹, and it lies ventral to the base of the lateral rostral process. The tubules of these ampullæ all run ventrally and pass internal to the supramaxillary furrow. There two tubules separate from the others, and running mesial to the external nasal aperture open on the external surface immediately ventro-mesial to that aperture. The remaining tubules of the group pass postero-lateral to the external nasal aperture, and open along the ventral edge of the nasal portion of the naso-labial fold. These ampullæ and their tubules all lie internal to the inner layer of the subepidermal membrane, but they are surrounded by delicate connective tissues that would seem to represent the corresponding layer of the corium.

Closely related to the ampullary pores on the ventral surface of the snout, there are several patches of small depressions which are the external openings of little glandular structures that are of epidermal origin and form little protuberances on the internal surface of the epidermis, suggesting undeveloped or degenerate ampullæ.

The subepidermal membrane in which, as above described, the larger part of the ampullary tubules lie is formed by the outer fibrous layer of the corium. The latero-sensory grooves, and the calcified cartilaginous rings that partly surround and support them, all lie external to this fibrous layer, as Wright (1884, p. 263) says that the latero-sensory canals of embryos of *Amblyurus* also do to the corresponding layer in that fish. The membrane passes external to the three rostral processes, and there encloses a median, three-sided space which lies between the three processes. The membrane is here thick, because of the accumulation of the enclosed ampullary tubules and sacs, and the inner layer of the membrane is markedly reticulated, the meshes in the membrane being traversed by the tubules of certain of the ampullæ and by the nerves that supply the others. The median portion of the three-sided space is filled with loose fatty connective tissue, and the nervus ophthalmicus superficialis of either

side, after issuing from the anterior opening of the ethmoidal canal, enters this space and there breaks up into numerous terminal branches. The two layers of the membrane extend into the supramaxillary fold, and apparently end in its ventro-anterior edge. The tubules of the outer buccal group of ampullæ open on the external surface oral to the supramaxillary fold, and they and the related sacs lie internal to the membrane that lodges the other tubules, but, as already stated, fibrous subdermal tissues are found in the lips and the naso-labial folds that seem to correspond to this layer of the corium, but they do not form a definite membrane.

In my work on *Mustelus* (Allis, 1901) no attention was given to the relations of the ampullæ to this fibrous membrane, but I now find, on re-examining my sections of this fish, that the conditions there are strictly similar to those in *Chimera*. In the work on *Mustelus* I came to the conclusion that each ampullary pore of the adult fish indicated, approximately, the place of origin of the related ampullary organ, the long ampullary tubule of certain of these organs being formed by an exceedingly rapid growth of a primarily short tube, that tube being stretched out between the two relatively fixed points represented by the surface pore and the point where the sensory nerve enters the organ. This has been since confirmed by Coggi (1902), and is further confirmed by the conditions that I have since found in *Chlamydoselachus*, the ampullæ of that fish all having short tubes, and the ampullary sacs all lying immediately beneath the related surface-pores. This marked difference in the positions of the ampullary sacs in this fish and those in *Mustelus* and *Chimera* evidently needs explanation, and it would seem as if it must be in some way related to the amount of cranial flexure at the time the ampullæ are developed. When the cranial flexure is at its greatest, those portions of the external surface of the head on which the ampullary pores are found in the adult must lie anterior or ventral to the curved anterior end of the central nervous system, and hence in the region of the future rostrum. If the ampullary sacs and the related nerves were well developed at this time, it would seem as if the tendency would be to hold the sacs there when the cranial flexure was later reduced and the brain drawn relatively backward. The dermal tissues would, on the contrary, probably retain their relative relations to the underlying parts of the brain, and hence also be drawn backward; and if the ampullæ had already penetrated the fibrous layer of the corium and continued to lie in it, their short tubes would be drawn out into long tubules lying in the fibrous layer of the corium, as is actually the case in *Mustelus* and *Chimera*. But if the ampullary sacs were not well developed when the cranial flexure was at its greatest, their tubules could not be stretched, and it would be the related nerve strands that would be lengthened, as in *Chlamydoselachus*. This would not, however, explain why these organs penetrate the fibrous layer of the corium without wholly perforating it, nor why these organs alone

enter this layer, the latero-sensory organs and terminal buds all lying external to it, as do apparently also the corresponding tissues of the ear and eye.

CONCLUSIONS.

In the chondrocranium of the adult *Chimera* the trabeculae arise from the ventral surface of the parachordals at a considerable distance posterior to their anterior ends, and they project antero-ventrally at a marked angle to the parachordals. This shows that there was not only marked cranial flexure at the time the trabeculae began to chondrify, but also that this flexure was not, as in the Plagiostomi, later greatly reduced; for that there has here been reversion from the conditions found in the adult Plagiostomi, the cranial flexure being first reduced and then later reacquired, seems wholly improbable. The Holocephali must accordingly be descended from some form in which conditions existed similar to those that are now found in embryos of the Plagiostomi, and as these conditions were probably not found in any adult form, the Holocephali must be descended directly from embryos of the Plagiostomi by conservation and modification of the conditions there found.

The chondrocranium is generally considered to have been formed as a cast which lies between the brain, as a core, and the external epidermis, the form of the cast depending primarily upon the form of the brain. There must accordingly have been some potent influence determining, in these fishes, the retention, by the forebrain, of the position imposed upon it by the marked cranial flexure of embryos. The precocious development of the eyeballs, and their shifting forward and mesially dorsal to the forebrain, where they are actually found in the adult, would doubtless have furnished such an influence; but, unfortunately for this assumption, Schauinsland's descriptions of *Callorhynchus* show that the eyeballs are still widely separated from each other in early embryonic stages, and that the midbrain lies between them. It would accordingly seem as if the determining influence, whatever it may have been, must have been related either to a precocious development of the olfactory organs, or to such a development of the functional mouth.

In all embryos of the Plagiostomi the mouth is at first directed ventrally, and if it became functional before the cranial flexure was reduced, it would evidently tend to remain ventral, this possibly explaining why it is found in this position in the adults of most of these fishes. If in such an embryo the cranial flexure were relatively late in being reduced, or, what is the same thing, if the mouth became precociously functional, the perpetuation of the conditions then existing might give rise to the relations of trabeculae to parachordals actually found in the adult Holocephali. The eyeballs would then naturally tend to shift forward, and when the head was later compressed latero-mesially they would lie dorsal to the forebrain. The other peculiarities of the

chondrocranium would then arise as a result of the anterior ends of the trabeculae turning dorsally anterior to the forebrain and between the nasal sacs, and then again forward in their terminal portions, represented in the median rostral process.

The peculiar form of the chondrocranium of these fishes would not then be primarily due to developmental adjustments to feeding habits, but to the acquisition of feeding habits adapted to anatomical conditions which were wholly independent of those habits.

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EXPLANATION OF THE PLATES.

The figures are all *natural size*.

PLATE I.

- Fig. 1. Lateral view of the head of *Chimera collicii*, showing the latero-sensory canals and the ampullary pores.
2. Median view of the bisected skull.

PLATE II.

- Fig. 3. Lateral view of the skull, with the labial and nasal cartilages in place.
4. Lateral view of the anterior end of the skull, with the ala nasalis and the cartilage *l* in place but the other labial and nasal cartilages removed.
5. The same, with the ala nasalis and cartilage *l* removed.
6. Ventro-anterior view of the end of the snout.

PLATE III.

- Fig. 7. Dorsal view of the skull.
8. Ventral view of the skull.
9. Posterior view of the skull.

Index Letters.

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| <i>a</i> , cartilage <i>a</i> of Hubrecht's descriptions. | <i>md</i> , mandibula. |
| <i>ab</i> , foramen for nervus abducens. | <i>mdl</i> , mandibular labial. |
| <i>acr</i> , foramen for arteria centralis retina. | <i>mlf</i> , mandibular labial fold. |
| <i>acv</i> , foramen for anterior cerebral vein. | <i>n</i> , process of cartilage <i>k</i> . |
| <i>adp</i> , anterior dental plate. | <i>nc</i> , nasal capsule. |
| <i>aec</i> , anterior opening of ethmoidal canal. | <i>nlf</i> , naso-labial fold. |
| <i>ant</i> , antorbital process. | <i>o</i> , foramen for nervus opticus. |
| <i>cav</i> , cavum cranii. | <i>obc</i> , outer buccalis latero-sensory canal. |
| <i>e</i> , cartilage <i>e</i> of Hubrecht's descriptions. | <i>ocm</i> , foramen for nervus oculomotorius. |
| <i>ec</i> , ethmoidal canal. | <i>opf</i> , foramen for nervus ophthalmicus profundus. |
| <i>epsb</i> , foramen for efferent pseudo-branchial artery. | <i>oph</i> , foramen for nervus ophthalmicus superficialis. |
| <i>f</i> , foramen for nerve and artery. | <i>pdp</i> , posterior dental plate. |
| <i>f'</i> , foramen for branch of nervus ophthalmicus. | <i>pec</i> , posterior opening of ethmoidal canal. |
| <i>fa</i> , foramen for nervus facialis. | <i>pf</i> , foramen for nervus palatinus facialis. |
| <i>fa</i> , fenestra nasalis. | <i>pfy</i> , perforation for pedicel of cartilage <i>fg</i> . |
| <i>fb</i> , foramen for branch of vena nasalis. | <i>pnb</i> , prenasal beak. |
| <i>fvn</i> , foramen for vena nasalis. | <i>pnd</i> , prenasal depression. |
| <i>g</i> , cartilage <i>g</i> of Hubrecht's descriptions. | <i>pq</i> , palatoquadrate. |
| <i>hmc</i> , hyomandibular latero-sensory canal. | <i>pre</i> , premaxillary lip. |
| <i>hmf</i> , foramen for nervus hyoideo-mandibularis facialis. | <i>pst</i> , postorbital process. |
| <i>hy</i> , hypophysial groove. | <i>ptf</i> , pituitary fossa. |
| <i>k</i> , cartilage <i>k</i> of Hubrecht's descriptions. | <i>pul</i> , posterior upper labial. |
| <i>lrp</i> , lateral rostral process. | <i>pv</i> , foramen for pituitary vein. |
| <i>m</i> , cartilage <i>m</i> of Hubrecht's descriptions. | <i>smcf</i> , supramaxillary fold. |
| | <i>soc</i> , supraorbital latero-sensory canal. |
| | <i>sos</i> , suborbital shelf. |
| | <i>subc</i> , suborbital latero-sensory canal. |
| | <i>t</i> , foramen for nervus trochlearis. |
| | <i>tr</i> , foramen for nervus trigeminus. |